Rubiacearum Americanarum Magna Hama Pars II. New and Newly Circumscribed Taxa of *Guettarda* (Guettardeae)

Charlotte M. Taylor
Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, U.S.A.
charlotte.taylor@mobot.org

David H. Lorence
National Tropical Botanical Garden, 3530 Papalina Road, Kalaheo, Kauai, Hawaii 96741, U.S.A. lorence@ntbg.org

ABSTRACT. The new species *Guettarda davidseorum* Lorence and *G. subcapitata* C. M. Taylor, here described and illustrated, are known from a moist forest region in Belize and dry forest regions from southern Mexico to Nicaragua, respectively. *Guettarda davidseorum* is similar in aspect to *G. deamii* Standley, and *G. subcapitata* has been previously confused with *G. macrosperma* Donnell Smith. Also considered here are distinctive patterns of variation in the wide-ranging variable species *G. crispiflora* Vahl, which support the recognition of five subspecies with generally allopatric geographic distributions; several of these subspecies differ from those that have been previously circumscribed.

RESUMEN. Las especies nuevas *Guettarda davidseorum* Lorence y *G. subcapitata* C. M. Taylor, aquí descritas e ilustradas, han sido registradas de bosques húmedos en Belice y de bosques secos del sur de México a Nicaragua, respectivamente. *Guettarda davidseorum* es similar en su aspecto a *G. deamii* Standley, y *G. subcapitata* se ha confundido con *G. macrosperma* Donnell Smith. Además se consideran aquí los patrones de variación en la pubescencia de la especie *G. crispiflora* Vahl, que es variable y de amplia distribución; estos patrones distintivos justifican la delimitación de cinco subespecies con distribuciones geográficas generalmente alopátricas, y varias de estas subespecies difieren de las que se han delimitado previamente.

Key words: Belize, *Guettarda*, Guettardeae, Mesoamerica, Mexico, Nicaragua, Rubiaceae.

Guettarda L. (Guettardeae) comprises about 80 (Steyermark, 1974) to more than 140 (cf. Andersson, 1992) species found in the Neotropics, Asia, Madagascar, and the Mascarenes. This genus is characterized by its axillary inflorescences, calyx limbs that are truncate or irregularly to regularly 2- to 9-lobed or -denticulate, salverform to tubular corollas with 4 to 9 quincuncial lobes that are sometimes crisped to appendaged on the margins, 4 to 9 stamens, and drupaceous fruits with a single 2- to 9-celled pyrene. Some species have distinctive sublineolate (i.e., closely set and subparallel) tertiary leaf venation and/or scorpioid cymes, and the flowers are frequently distylous. The neotropical members of this genus have not been treated taxonomically together in this century, but Steyermark (1972) reviewed the genus in detail for northeastern South America and also presented a partial taxonomic treatment for some species found in adjacent regions.

During study of *Guettarda* for the *Flora Mesoamericana*, the following new species were discovered. Also, review of recently collected specimens showed that Steyermark's (1972) delimitation of the common species *G. crispiflora* Vahl and its infraspecific taxa is in need of reconsideration.

NEW SPECIES OF *GUETTARDA*

Guettarda davidseorum Lorence, sp. nov. TYPE: Belize. Toledo: Southern Maya Mountains, Bladen Nature Reserve, mountains 1.7 airline km N of the Ek Xux archeological site, 16°31′05″N, 88°54′11″W, 450 m, 24 May 1996 (fl), *G. Davidse 36271* (holotype, MO-5174713; isotypes, BM, MEXU, PTBG). Figure 1.

Haec species *Guettardae deamii* Standley affinis, sed ab ea pubescentia strigillosa, lamina foliari minore 1.5–4.5 × 0.7–1.8 cm, inflorescentia 1–3-flora pedunculo sericeo 1.5–3 mm longo insidente atque lobulis corollinis minoribus 1.5–2 mm longis differt.

Slender shrubs to 3 m tall; leafy twigs 0.7–1 mm diam., densely strigillose with ascending fulvous trichomes, soon glabrescent and becoming blackish brown. *Leaves* opposite but crowded at ends of twigs, mostly isophyllous, (1)1.5–4.5 × (0.5)0.7–

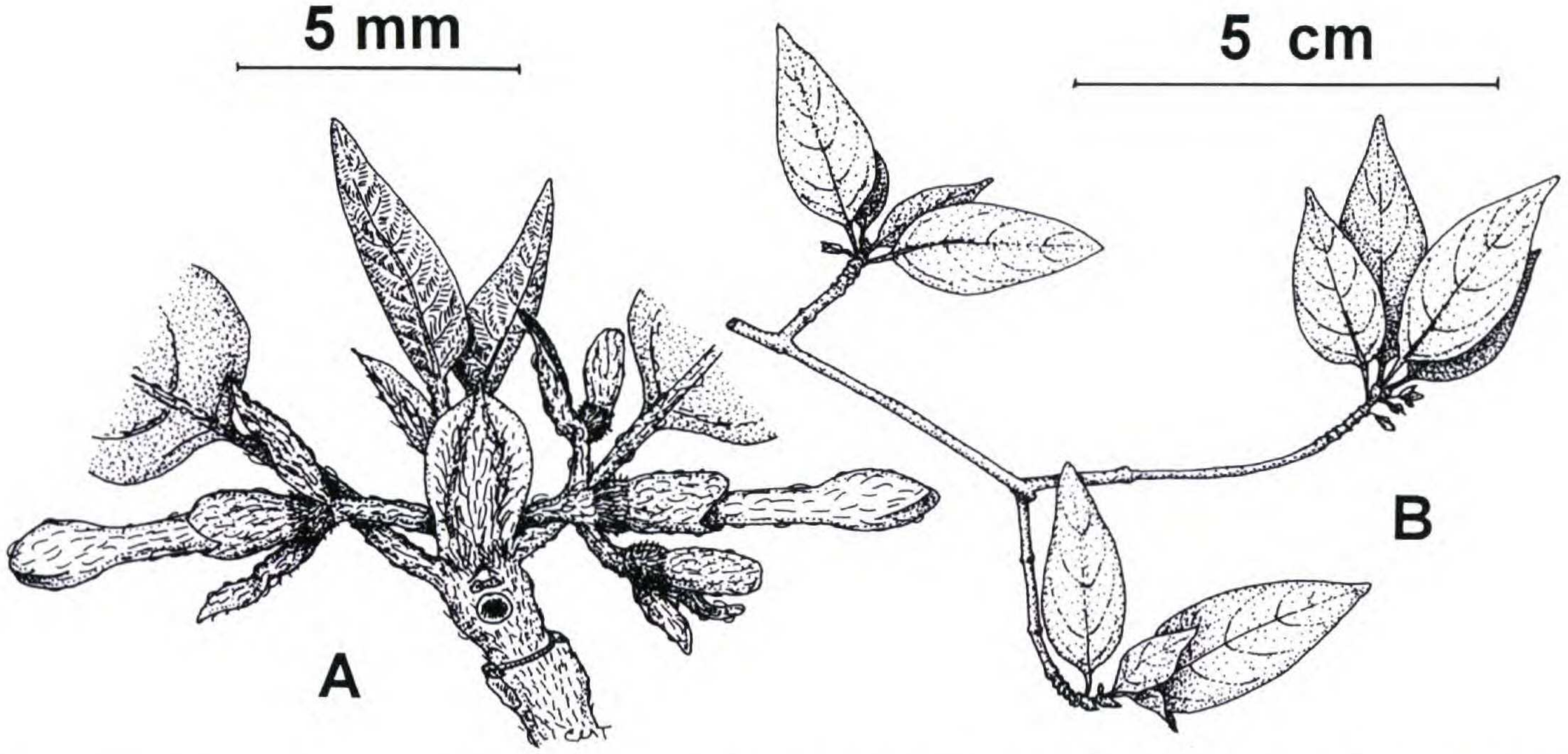

Figure 1. *Guettarda davidseorum* Lorence; based on *Davidse et al. 36271.*—A. Stem apex showing inflorescences with unopened flower buds. —B. Flowering branch.

1.8 cm, ovate to ovate-elliptic or ovate-lanceolate, drying chartaceous and discolorous, adaxially sparsely strigillose with the pubescence denser on the costa and secondary veins, abaxially densely pale brown- or fulvous-sericeous with silky trichomes concealing the surface, at base cuneate to rounded or sometimes subtruncate, at apex acute to short-acuminate; secondary veins 4 to 6 pairs, looping to interconnect, the tertiary veins subparallel, the quaternary veins reticulated within the tertiary areoles, adaxially the venation prominulous, abaxially the costa prominent, the secondary veins prominulous, and the minor venation apparently plane; *petioles* (1)2–7 × 0.3–0.4 mm, densely strigillose; *stipules* interpetiolar, 2.5–4.5 × 1–2 mm, obovate-elliptic to oblong-lanceolate, obtuse, mucronulate, externally strigillose, internally glabrous, caducous. *Inflorescences* 1 per axil, densely sericeous, with flowers solitary or 2 to 3 in a cyme to 1 cm long (including corollas); peduncles 1.5–3 mm long. *Flowers* sessile or with pedicels to 1 mm long, the lateral flowers when present subtended by 1 to 3 bracteoles 2–3 mm long, linear-oblong; hypanthium 0.5–0.7 mm long; calyx limb 1.5–2 mm long, tubular-spathaceous, split along one side or shallowly 2-lobed, externally sericeous, internally glabrous; corolla salverform, white, externally antrorse strigillose-sericeous, tube ca. 6 mm long, ca. 0.6 mm diam. near middle, lobes 4, 1.5–2 × 0.5–0.8 mm, elliptic to oblong; stamens inserted ca. 0.5 mm below top of tube, anthers ca. 1 mm long, partially exserted; style ca. 3 mm long, stigma capitate, included. *Fruits* unknown.

Distribution, habitat, and phenology. In lowland, moist, tall forest at 450 m in a saddle between volcanic- and limestone-derived mountains in southwestern Belize; collected in flower in May.

This new species is known only from the type collection. It is distinguished from other Mesoamerican *Guettarda* species by its smaller inflorescences with very short peduncles and corollas with small lobes. It is similar in general aspect to *Guettarda deamii*; *G. deamii* differs by its spreading pilose pubescence, larger leaves (4–8 × 2.5–6.5 cm) with more numerous secondary veins (8 to 10 pairs), 3- to 5-flowered inflorescences with longer pilose peduncles (3–10 mm long), and larger corolla lobes (3–4 mm long). I take pleasure in naming this new species for its collector, Gerrit Davidse, coordinator of the *Flora Mesoamericana* project, and his wife and collaborator Jeany Davidse, in recognition of their extensive contributions to neotropical botany.

Guettarda subcapitata C. M. Taylor, sp. nov. TYPE: Mexico. Chiapas: Km 18–22 de la carretera Tuxtla Gutiérrez–Cañón del Sumidero, 10 Apr. 1983 (fl), *O. Tellez & J. S. Villaseñor 6689* (holotype, MEXU; isotype, MO-3331819). Figure 2.

Haec species a congeneris limbo foliari subtus pubescentia secus costam etiam nervae secundarios patente ceterum adpressa vestito, inflorescentiis pedunculatis congesto-cymosis vel subcapitatis et foliis juvenilibus simultaneis, corollae tubo 9–13 mm longo ac lobulis 4–6 atque fructu 10–14 mm longo distinguitur.

Shrubs or trees to 7 m tall, apparently deciduous; branchlets densely strigulose to velutinous. *Leaves*

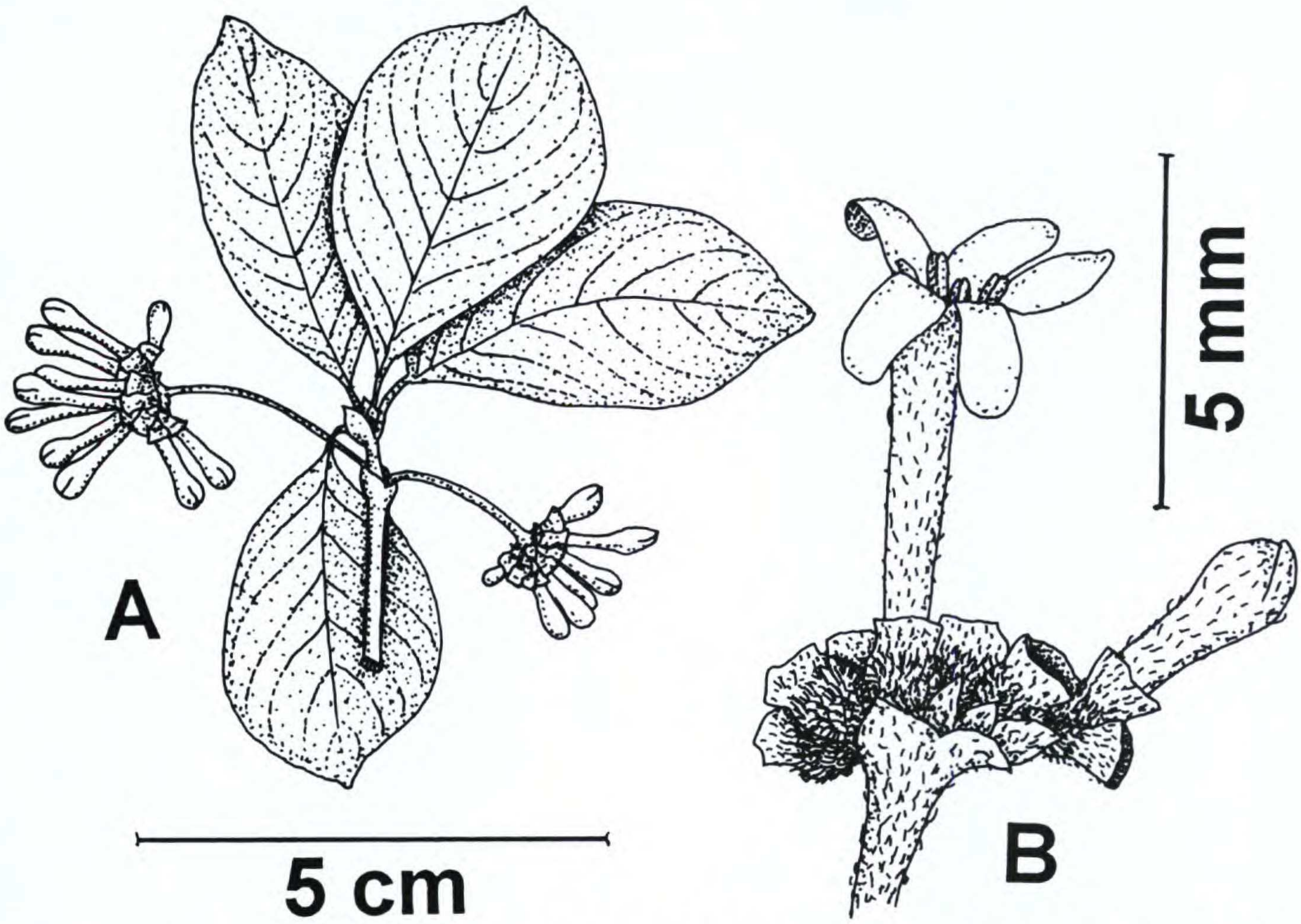

Figure 2. *Guettarda subcapitata* C. M. Taylor; based on *Téllez & Villaseñor 6609.*—A. Flowering branch. —B. Detail of inflorescence with 7 to 11 flowers, showing 1 unopened flower bud, 1 open flower, and 6 old flowers from which the corolla has fallen.

elliptic to elliptic-oblong or lanceolate, 2–10 × 1.3–7 cm, papyraceous, adaxially sparsely to moderately pilosulous to hirtellous, abaxially hirtellous on costa and secondary veins and strigulose to pilosulous on minor venation but glabrous on blade surface, at base cuneate to obtuse, at apex obtuse to acute or rarely subrounded; secondary veins 5–7 pairs, loosely looping to interconnect, with barbate domatia in axils, tertiary veins subparallel to areolate, quaternary veins reticulated inside tertiary areoles, adaxially venation plane, abaxially costa and secondary veins prominulous and remaining venation plane; *petioles* 5–12 mm long; *stipules* interpetiolar, caducous or sometimes persistent with leaves, triangular, 3–7 mm long, acute to acuminate, externally densely strigulose to sericeous. *Inflorescences* 1 per axil, subcapitate to congested cymose and shortly dichotomous, 7- to 11-flowered; peduncle 0.9–3.5 cm long; bracts none or few, narrowly ligulate, 1–9 mm long, obtuse to rounded. *Flowers* sessile; hypanthium turbinate to cylindrical, 1.5–2 mm long, densely velutinous; calyx limb 1–2.5 mm long, densely hirtellous-velutinous, truncate to shortly and irregularly 2- to 4-lobed; corolla salverform, white, externally antrorse-strigulose to -velutinous, tube 9–13 mm long, lobes (4)5(6), oblong-elliptic, 3.5–5 mm long, obtuse to rounded, plane or a little crisped; anthers ca. 3 mm long, partially exserted; stigmas capitate, ca. 0.3 mm long, situated near middle of corolla tube. *Fruits* subglobose, 10–14 mm diam., densely short-velutinous, with an apical calyx limb scar to 6 mm diam.; pyrenes smooth, 4-locular.

Distribution, habitat, and phenology. Deciduous and semideciduous dry forests and seasonal evergreen forests at 30–1350 m, southern Mexico to central Nicaragua; collected with flowers March–June, in fruit January and July–November.

This new species has been confused with *Guettarda gaumeri* Standley and *G. macrosperma*; *G. subcapitata* can be distinguished from both of these by its apparently deciduous habit, leaves with the pubescence on the abaxial surface mostly appressed except spreading on the costa and secondary veins, inflorescences that are produced together with the flush of new leaves and are congested-cymose to subcapitate, peduncles 0.9–3.5 cm long, corolla tubes 9–13 mm long, corolla lobes 4 to 6 (but usually 5), and fruits 10–14 mm diam. In con-

trast, *G. gaumeri* has inflorescences produced when the leaves are already fully developed, appressed pubescence on the abaxial leaf surface, peduncles absent or up to 8 mm long, corolla tubes 6–8 mm long, and fruits 5–7 mm long; and *G. macrosperma* has inflorescences also produced when the leaves are already fully developed, leaves with the abaxial surface glabrous except with appressed-strigillose pubescence on the costa and secondary veins, inflorescences that are congested to rather expanded cymose with the axes evident, and fruits 18–20 mm diam. The specific epithet refers to the distinctive inflorescence arrangement. In all the flowers studied the anther position, style length, and stigma position are similar to those of short-styled flowers of other species of *Guettarda*, so it is possible that *G. subcapitata* is also distylous.

Paratypes. EL SALVADOR. **La Libertad:** Chiltiupan, *Allen & Armour 7329* (F); Deninger, *Current 3* (MO); cantón El Platanillo, Quezaltepeque, *Villacorta 1082* (LAGU, MO). **Santa Ana:** municipio de Santa Ana, faldas del Cerro Las Mesas, ca. 10 km al NO de la ciudad de Santa Ana, 14°02′30″N, 89°36′W, *Linares & Martínez 2625* (MO); El Pinalito, Santa Ana, *Villacorta 2206* (LAGU, MO). GUATEMALA. **Escuintla:** La Trinidad, on road between Escuintla and Finca Zapote, *Standley 64825* (F). **Jutiapa:** 7 km NE of Jutiapa on CA-1, *Harmon & Dwyer 3339* (MO). **Sacatepeque:** 2.3 mi. SW of Alotenango on road from Antigua to Escuintla, *Croat 42013* (MO). **Santa Rosa:** near Cerro Redondo, *Standley 60413A* (F). HONDURAS. **Comayagua:** Las Limas, *Edwards P604* (F); vicinity of Siguatepeque, *Standley & Chacón 6794* (F). **Francisco Morazán:** Tegucigalpa, alrededores aldea Suyapa, quebrada La Barranca, *E. Romero 62* (MO). **Ocotepeque:** Lempa River, road to Esquipulas, *Molina 22432* (F); along Lempa River between Santa Anita and Santa Fé, *A. Molina R. & A. R. Molina 31051* (MO). MEXICO. **Chiapas:** municipio de Berriozábal, 5 km E of Berriozábal along Mexican Highway 190, *Breedlove 20374* (F, MO); municipio de Tuxtla Gutiérrez, El Sumidero, 22 km N of Tuxtla Gutiérrez, *Breedlove & Smith 21594* (F); municipio de Chiapa de Corzo, at Río Grijalva, 10 km W of Chiapa de Corzo, along Mexican Highway 190, *Breedlove 26239* (MO); municipio de Berriozábal, on flats near Berriozábal, *Breedlove 50630* (MO); El Aguacero, 13 km al NO de Ocozocoautla, *E. Cabrera & H. de Cabrera 7883* (MEXU, MO); municipio de Amatenango de la Frontera, El Sabinalito, a 14 km al SO de Motozintla, camino a Amatenango, 15°25′N, 92°07′30W, *E. Martínez S. et al. 22383* (PTBG); municipio de Ocozocuautla, canyon on Rio de la Venta at Cascada El Aguacero, 16°46′N, 93°33′W, *Neill 5566* (MO); municipio de Chiapa de Corzo, El Correadero, 5.6 mi. SE of Chiapa de Corzo, along Mexican Highway 190, *A. Shilom Ton 2962* (F). NICARAGUA. **Estelí:** Llano Redondo, *Laguna 363* (MO); along Estanzuela Creek, 8 km W of Estelí, *A. Molina R. 23081* (F); Paso León, 4 km al NE de la ciudad de Estelí, 13°7′N, 86°20′W, *Moreno 24158* (MO); La Estanzuela, 6 km al S de la ciudad de Estelí, 13°1′N, 86°21′W, *Moreno 24174* (MO); El Porvenir, 7 km al N de la ciudad de Estelí, 13°9′N, 86°22′W, *Moreno 24193* (MO). **Jinotega:** along Tuma Lake N of Jinotega, *Williams et al. 27499* (F).

The "*Guettarda crispiflora*" Complex

Steyermark (1971, 1972) was the first taxonomist to formally note that a distinctive group of commonly collected, widely distributed, and frequently confused *Guettarda* species actually comprise a single widespread species whose reproductive characters are remarkably consistent throughout its range. Based on careful study of specimens from across northern South America and the Antilles, he included a number of poorly characterized names as synonyms of *Guettarda crispiflora* Vahl, which is based on a type from Montserrat. These plants are handsome, small to medium-sized trees that are frequently encountered in flower in secondary vegetation in wet forest zones, typically at middle to higher elevations but also to as low as sea level in particularly wet zones. The inflorescences are markedly scorpioid and typically spreading to pendulous so they are visible below the leaves. The flowers are showy, sweetly fragrant, and distylous, with the corollas pale to dark pink with crisped lobes. The ripe fruits are succulent and blue-black to black.

Steyermark's broad circumscription of *G. crispiflora* comprised two subspecies and four varieties, all based on morphological details that were correlated with geographic range. In this work Steyermark focused on the plants of northeastern South America, but he also considered the plants of adjacent regions. In his classification, *G. crispiflora* subsp. *crispiflora* was found in the Lesser Antilles and the coastal cordillera of northern Venezuela, while *G. crispiflora* subsp. *discolor* (Rusby) Steyermark was found in the Sierra de Santa Marta of northern Colombia and the Andes of Colombia and Ecuador. Within each of these subspecies, he recognized two allopatric varieties. Steyermark considered the number and degree of development of calyx lobes and the pubescence, particularly its distribution on the leaves, to be taxonomically important in *G. crispiflora*, but noted that number of locules in the ovary and fruits were variable and not particularly informative.

Numerous additional specimens are available today from regions adjacent to Steyermark's study area, and show that Steyermark's broad circumscription of *Guettarda crispiflora* is justified. The collections show also that his classification system is in need of expansion and some realignment, to include the plants of Mesoamerica and those of the Andean Cordillera south to Bolivia. Most of the morphological features that were previously used to

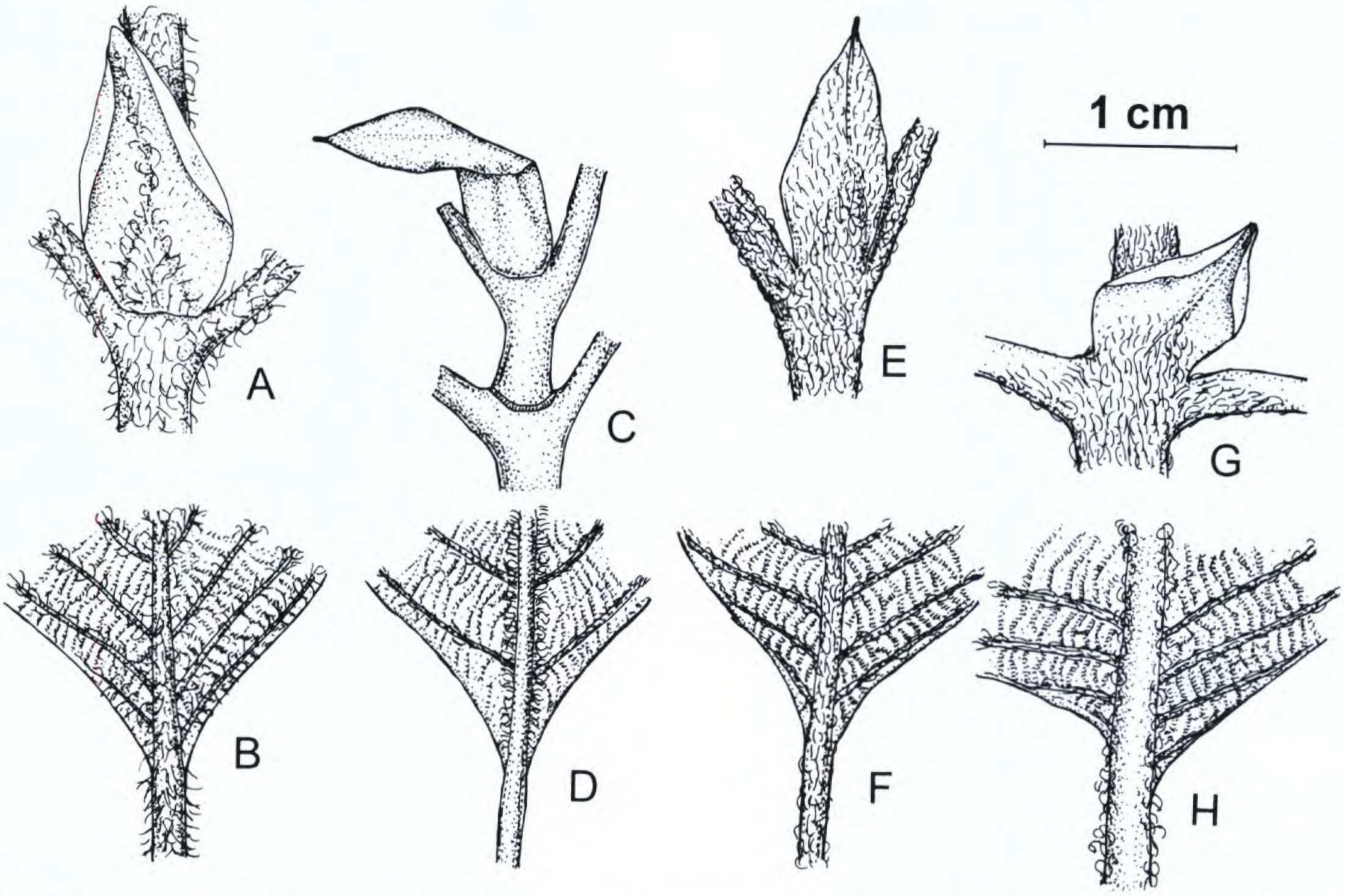

Figure 3. Details of pubescence of four subspecies of *Guettarda crispiflora* Vahl. A, B, *G. crispiflora* subsp. *cobanensis*; based on *Nee 407*.—A. Stipule and stem node. —B. Leaf base and distal portion of petiole. C, D, *G. crispiflora* subsp. *poasana*; based on *Fosberg 47826*.—C. Stem apex showing stipule and two stem nodes. —D. Leaf base and distal portion of petiole. E, F, *G. crispiflora* subsp. *sabiceoides*; based on *Porter 4416*.—E. Stipule and stem node. —F. Leaf base and distal portion of petiole. G, H, *G. crispiflora* subsp. *crispiflora*; based on *Duss 949A*.—G. Stipule and stem node. —H. Leaf base and distal portion of petiole.

separate the species of the "*G. crispiflora* complex" can now be seen to vary continuously throughout this entire area, as discussed below, and no discontinuous variation is observable in any reproductive characters. However, several well-marked entities with clearly demarcated geographic ranges can be distinguished based on vegetative characters.

Although Steyermark relied primarily on calyx lobe length to separate his infraspecific taxa, with more specimens now available this feature does not seem to be informative. Steyermark did not use the total length of the calyx limb, which is 0.8–1.2 mm long in plants from throughout the range of this species, but rather the proportion that is lobed. However, this proportion of lobing is variable and its variation seems to be continuous and uncorrelated with geographic distribution or any other character, so when recent collections are considered his keys no longer work. Here five subspecies are distinguished primarily based on patterns of pubescence type, density, and distribution on the plant; no other characters show clear patterns of variation. These pubescence characters (Fig. 3) are remarkably consistent and closely correlated with geographic distribution; in some cases, details of the leaf shape are also distinctive. The distinctions, characteristics, nomenclature, and geographic ranges of these subspecies are summarized in the key and taxonomic treatment below.

Each of the subspecies of *Guettarda crispiflora* is most similar in general aspect and some morphological features to the geographically adjacent subspecies. The rather close relationships among the subspecies are shown by the subtle nature of their distinctions, the narrow zones of intergradation between some of them, and the sporadic occurrence of plants with characteristics of one subspecies deep within the range of another subspecies. For example, the plants of the Lesser Antilles (subsp. *crispiflora*) are most similar in general aspect to those of northern Central America (subsp. *cobanensis*); the plants of northern Costa Rica (subsp. *poasana*), long treated as a separate species because of their striking, mostly glabrous appearance, overlap or intergrade in a narrow zone in central Costa Rica with the densely pubescent plants found in southern Costa Rica (subsp. *sabiceoides*); and individual

plants that are mostly glabrous, similar to subspecies *poasana*, occur sporadically throughout the range of the species (e.g., Colombia, *Gentry et al. 55267*, MO; Bolivia, *Solomon 13993*, MO).

KEY TO THE SUBSPECIES OF *GUETTARDA CRISPIFLORA*

1. Leaves (at least when young) abaxially densely, closely tomentulose on the areoles, with the blade surface not visible, and sparsely strigillose on the veins including the higher-order venation; northern Venezuela through the Sierra de Santa Marta and the Western Andean Cordillera of Colombia . . . . . c. subsp. *discolor*
1′. Leaves (at least when young) abaxially glabrous on the areoles, with the blade surface visible, and sparsely to densely strigillose to sericeous on the veins including the higher-order venation; Lesser Antilles, Central America, and western Colombia south to Bolivia.
   2. Petioles and stems with the surface not visible, densely strigillose to sericeous or pilosulous to hirsutulous with closely appressed to spreading, densely tangled trichomes; central Costa Rica to Colombia and south through the Andean Cordillera to Bolivia . . . . . e. subsp. *sabiceoides*
   2′. Petioles and stems with the surface visible, glabrous or hirsutulous to pilosulous with spreading tangled trichomes.
      3. Petioles and stems glabrous, or sparsely strigillose when young becoming glabrous with age; northern Costa Rica . . . . . d. subsp. *poasana*
      3′. Petioles and stems hirsutulous to pilosulous with spreading, tangled trichomes; Lesser Antilles and Guatemala to northern Costa Rica.
         4. Leaf bases obtuse to cuneate or acute and often with sides concave; Guatemala to northern Costa Rica. . . . . b. subsp. *cobanensis*
         4′. Leaf bases broadly obtuse to truncate; Lesser Antilles . . . . . a. subsp. *crispiflora*

Guettarda crispiflora Vahl, Eclog. Amer. 36, t. 6. 1796. TYPE: [Lesser Antilles,] Montserrat, *Ryan s.n.* (holotype, C not seen).

a. Guettarda crispiflora subsp. **crispiflora.** Figure 3G, H.

Illustration: Fournet (1978: 1194, fig. 589).

This subspecies is characterized by spreading pubescence and leaves with the bases broadly obtuse to truncate; it is found in the Lesser Antilles [Montserrat, Guadeloupe, Dominica, Martinique, St. Lucia, St. Vincent, and Grenada (Howard, 1989)]. As circumscribed here, this subspecies corresponds to *Guettarda crispiflora* subsp. *crispiflora* var. *crispiflora* of Steyermark (1972: 367–368; Steyermark omitted the typical variety in his nomenclatural citations, but mentioned it in his subsequent discussion). Relatively few specimens of this subspecies have been seen, and it is not clear from these if the Antillean plants are distylous. Loss of distyly has been observed in some species of *Palicourea* in the Antilles (Taylor, 1993) and is presumed to indicate isolation of these plants from conspecific distylous populations on the mainland.

b. Guettarda crispiflora subsp. **cobanensis** (Donnell Smith) C. M. Taylor, comb. et stat. nov. Basionym: *Guettarda cobanensis* Donnell Smith, Bot. Gaz. 47: 255. 1909. TYPE: Guatemala. Alta Verapaz: near Cobán, 1500 m, *von Tuerckheim II.2096* (holotype, US not seen, microfiche). Figure 3A, B.

This species is characterized by spreading pubescence and leaves with the bases obtuse to cuneate or acute; it is found in Guatemala, Nicaragua, and northern Costa Rica.

c. Guettarda crispiflora subsp. **discolor** (Rusby) Steyermark, Acta Bot. Venez. 6: 130. 1971. *Guettarda discolor* Rusby, Descr. N. Sp. S. Amer. Pl. 134. 1920. TYPE: Colombia. Sierra del Libano, region of Santa Marta, 1650 m, 2 Mar. 1898–1899, *H. H. Smith 1809* (holotype, NY not seen, microfiche).

Guettarda steyermarkii Standley, Fieldiana, Bot. 28(3): 576, fig. 125A-B. 1953. Syn. nov. TYPE: Venezuela. Mérida: steep NW- and NE-facing slopes above "La Isla," above Tabay, 2285–2745 m, 18 May 1944, *J. A. Steyermark 56601* (holotype, F).

Guettarda crispiflora subsp. *crispiflora* var. *venezuelensis* Steyermark, Acta Bot. Venez. 6: 129. 1971. TYPE: Venezuela. Aragua: Colombia Tovar, 1900–2000 m, 25 Dec. 1921, *H. Pittier 9967* (holotype, VEN not seen).

Guettarda steyermarkii fo. *pilosior* Steyermark, Acta Bot. Venez. 6: 131. 1971. TYPE: Venezuela. Mérida: 40 km ESE of Tabay, 5 km E of San Juan Bautista, 1000 m, 22 July 1953, *E. L. Little 15372* (holotype, VEN not seen).

Illustration: Steyermark (1974: 802, fig. 128).

This subspecies is characterized by leaves with the pubescence of the abaxial surface of mixed types, closely tomentulose on the areoles and sparsely strigillose on the veins; it is found in the coastal mountain ranges and the Western Cordillera of the Andes in Colombia and Venzuela. Steyermark (1972) distinguished *G. steyermarkii* from *G. crispiflora* by its leaves with "the lower surface . . . densely silvery-gray pubescent" and inflorescences branched twice ("4-branched," i.e., each axis divided and then divided again, vs. once or "2-

branched" in his circumscription of *G. crispiflora*) but noted that that *G. steyermarkii* may not actually be distinct from *G. crispiflora.* Twice-branched inflorescences are found only in a few specimens from Venezuela, and several specimens have both once- and twice-branched inflorescences (e.g., *Liesner 12732,* MO; *Hahn & Grifo 5072,* MO). Plants with twice-branched inflorescences are not distinguished by any other features, and the characteristic pubescence of the abaxial leaf surface noted by Steyermark for this species is the same as the pubescence that characterizes subspecies *discolor.* Therefore, *G. steyermarkii* is not recognized here.

d. Guettarda crispiflora subsp. **poasana** (Standley) C. M. Taylor, comb. et stat. nov. Basionym: *Guettarda poasana* Standley, J. Wash. Acad. Sci. 18: 182. 1928. TYPE: Costa Rica. Alajuela: Viento Fresco, slopes of Volcán Poas, 1800 m, 13 Feb. 1926, *P. C. Standley & Torres 47807* (holotype, US not seen, photo PTBG). Figure 3C, D.

Illustration: Burger and Taylor (1993: 46, fig. 32).

This subspecies is characterized by its glabrous or sparsely strigillose petioles and stems; it is found in northern Costa Rica and intergrades in a narrow strip along the southern edge of its range with subspecies *sabiceoides.* Occasional specimens collected in this contact region show some pubescence features of each subspecies, with the strigillose pubescence characteristic of subspecies *poasana* distributed on the entire stipule and along the abaxial leaf midvein in the pattern characteristic of subspecies *sabiceoides.* These intermediate specimens are considered here to support the inclusion of *G. poasana* within the *G. crispiflora* complex. Because these plants are here considered intermediates between these two subspecies they cannot be keyed to a subspecies in the key above.

e. Guettarda crispiflora subsp. **sabiceoides** (Standley) C. M. Taylor, comb. et stat. nov. Basionym: *Guettarda sabiceoides* Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 291. 1928. *Guettarda crispiflora* subsp. *discolor* var. *sabiceoides* (Standley) Steyermark, Acta Bot. Venez. 6: 130. 1971. TYPE: Colombia. Cauca: forests of the Rio Palacé, highlands of Popayán, 1500–1800 m, *Lehmann B.T. 950* (holotype, K not seen). [Standley cited the type number incorrectly in his original description as "960," but this was later corrected by him (Standley, 1930), and this correction was noted by Steyermark (1971, 1972).] Figure 3E, F.

Guettarda conferta Bentham, Bot. Voy. Sulphur 106. 1845. TYPE: Costa Rica. Cocos Island, *Barclay s.n.* (holotype, BM).

Guettarda ochreata Schlechtendal, Linnaea 28: 496. 1856. TYPE: Peru. San Gavan, Aug. 1854, *Lechler in Hohenacker 2407* (holotype, B not seen, destroyed).

Guettarda pichisensis Standley, Publ. Field Columbian Mus., Bot. Ser. 8: 172. 1930. TYPE: Peru. Junín: Pichis Trail between San Nicolás and Azupuzú, 650–900 m, 6 July 1929, *E. P. Killip & A. C. Smith 26104* (holotype, F).

Guettarda chiriquiensis Standley, Ann. Missouri Bot. Gard. 25: 838. 1938. TYPE: Panama. Chiriquí: valley of upper Rio Chiriquí Viejo, 1300–1900 m, 27 July 1937, *P. White & G. White 22* (holotype, MO; isotypes, A not seen, F).

Guettarda cuatrecasasii Standley ex Steyermark, Acta Biol. Venez. 4: 56, fig. 25–26. 1964. TYPE: Colombia. Caquetá: Cordillera Oriental, vertiente oriental, bosque abierto en Cajón de Pulido, Quebrada del Río Hacha, 1700 m, 26 Mar. 1940, *J. Cuatrecasas 8737* (holotype, F; isotype, US not seen).

Guettarda sordida Standley ex Steyermark, Acta Biol. Venez. 4: 56, fig. 27. 1964. TYPE: Colombia. Caquetá: Cordillera Oriental, vertiente oriental, Quebrada del Río Hacha, abajo de Gabinete, 2100–2250 m, 23 Mar. 1940, *J. Cuatrecasas 8543* (holotype, F; isotype, US not seen).

Illustration: Burger and Taylor (1993: 46, fig. 32).

This subspecies is characterized by pubescence on the vegetative organs that is spreading to appressed and sometimes mixed but not in a consistent or distinctive pattern. It ranges from southern Costa Rica, where it intergrades in a narrow region with subspecies *poasana,* to Bolivia. This subspecies is variable in pubescence pattern generally throughout its range. The plants from the Andes of western Colombia to Bolivia may be better treated in more than one subspecies, but no consistent patterns are evident within this variation at present and these plants are provisionally combined here. For example, the entire range of variation in leaf size and pubescence characters that is found in subspecies *sabiceoides* throughout South America is also found among the plants from the relatively small Bajo Calima region of western coastal Colombia.

Two weakly distinguished patterns of pubescence are evident within Mesoamerican plants of subspecies *sabiceoides.* One of these, the "chiriquiensis" form, is characterized by hirsutulous to pilosulous pubescence throughout the petioles and abaxial leaf surfaces except on the abaxial costa, where the trichomes range from spreading to reflexed; this pubescence pattern is found on the type specimen of *Guettarda chiriquiensis.* Plants with this pubescence pattern are found sporadically in southern Costa Rica, occasionally on Cocos Island, common-

ly in the region of Volcán Chiriquí in western Panama, and infrequently in western Colombia and Ecuador. The other pubescence pattern, the "sabiceoides" form, is characterized by appressed, strigillose to sericeous pubescence, sometimes mixed with a few spreading trichomes, on the petioles and the abaxial leaf surfaces including the abaxial costa, though here the pubescence may become more spreading as the leaf ages; this pubescence pattern is found on the type specimen of *G. sabiceoides*. Plants with this pubescence pattern are found throughout the range of subspecies *sabiceoides*, and this is the most commonly collected pubescence pattern except in the region of the Volcán Chiriquí in Panama.

Guettarda conferta has been separated by previous authors (e.g., Burger & Taylor, 1993) based on its relatively low elevational distribution, 0–300 m, in very wet regions; its relatively numerous secondary leaf veins (12 to 16 pairs), though this condition is also found in occasional plants from higher elevations; and its shorter peduncles (to 1 cm), though this condition is also found in occasional plants from higher elevations. However, with more specimens now available, continuous variation can be found in all the features formerly used to separate this species, and it is not recognized here.

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Literature Cited

Andersson, L. 1992. A provisional checklist of neotropical Rubiaceae. Scripta Bot. Belg. 1: 1–199.

Burger, W. & C. M. Taylor. 1993. Flora Costaricensis. Family #202, Rubiaceae. Fieldiana, Bot. n.s. 33: 1–333.

Fournet, J. 1978. Flore Illustrée des phanérogames de Guadeloupe et de Martinique. Institut National de la Recherche Agronomique, Paris.

Howard, R. A. 1989. Flora of the Lesser Antilles: Leeward & Windward Islands. Vol. 6: Dicotyledons, Part 3. Arnold Arboretum, Jamaica Plain, Massachusetts.

Standley, P. C. 1930. The Rubiaceae of Colombia. Publ. Field Columbian Mus., Bot. Ser. 7(1): 1–175.

Steyermark, J. A. 1971. Rubiáceas nuevas de Los Andes y Cordillera de la Costa de Venezuela. Acta Bot. Venez. 6: 99–198.

———. 1972. *Guettarda. In:* B. M. Maguire & Collaborators, Flora of the Guayana Highlands. Mem. New York Bot. Gard. 23: 357–372.

———. 1974. Rubiaceae. *In:* T. Lasser (editor), Flora de Venezuela 9: 1–2070. Instituto Botánico, Dirección de Recursos Naturales Renovables. Ministerio de Agricultura y Cría, Caracas, Venezuela.

Taylor, C. M. 1993. Revision of *Palicourea* (Rubiaceae: Psychotrieae) in the West Indies. Moscosoa 7: 201–241.